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RESEARCH ARTICLE

Impact of the morphology of logged areas on medium and large mammal communities in forests

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Abstract

Context The morphology of logged areas (MLA) can impact medium and large mammal habitat. Assessing MLAs with landscape metrics facilitates sustainable forest management and biodiversity conservation.

Objectives We quantified MLAs and assessed their impacts on medium and large mammals.

Methods We assessed mammal occurrence using camera traps in 24 logged and 26 unlogged sites in South Korea and collected environmental variables, including nine MLA indices, at the microscale (50 m), mesoscale (500 m), and macroscale (1 km). After performing a principal component analysis (PCA), linear mixed and single-species occupancy models were used to assess the effects of principal components on mammal diversity and species-specific responses.

Results In the PCA results, MLA components were notably associated with spatial scales, with 50-m-scale indices separated from larger-scale indices. Several MLA components showed strong associations. Microscale MLA traits, particularly edge complexity and reduced unlogged patch connectivity, negatively affected diversity. At the species level, omnivores—specifically, wild boar (*Sus scrofa*) and Asian badger (*Meles leucurus*)—were negatively influenced by the same MLA component influencing diversity. In contrast, leopard cats (*Prionailurus bengalensis*) showed a preference for simplified spatial arrangements—characterized by fewer logged areas and short edges—at the 500 m and 1 km scales.

Conclusions Our findings highlight the importance of MLAs in mitigating logging impacts on mammals, as some morphologies can reduce exposure and

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provide more favorable habitat. Designing logged areas based on MLA indices can help balance conservation and resource use.

Keywords Biodiversity · Conservation · Logging · Forestry · Landscape morphology · Mammals

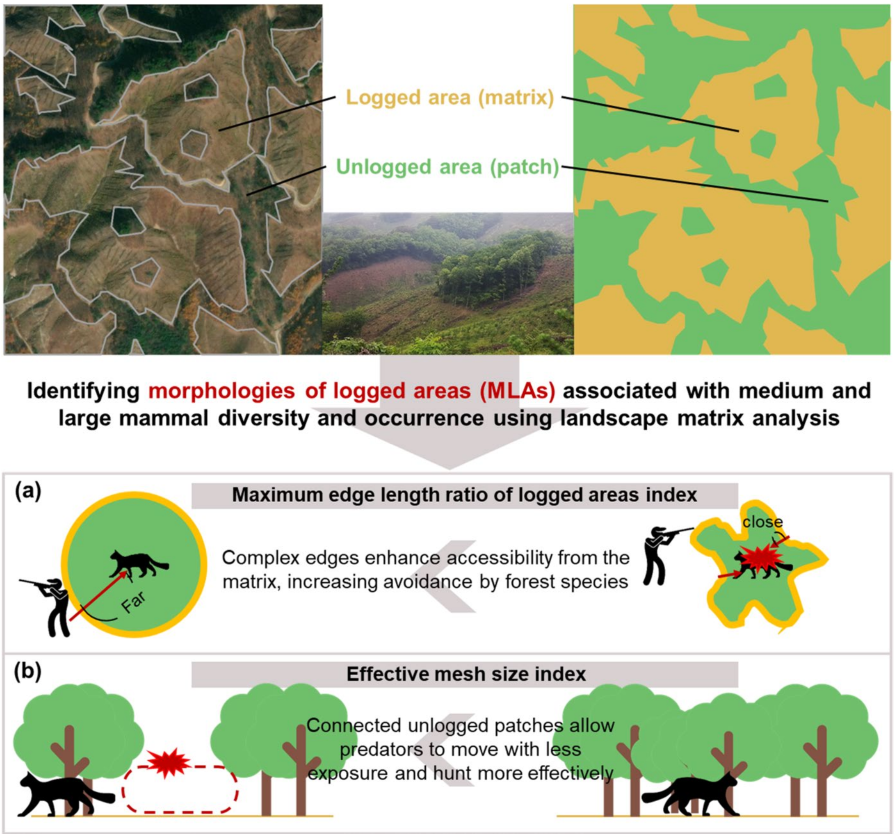
Abbreviations

MLA	Morphology of logged areas
LMM	Linear mixed models
VIF	Variance inflation factor

Introduction

Forestry practices, namely clear-cutting, widely used for resource extraction cause habitat fragmentation and increase environmental heterogeneity (Jamhuri et al. 2018; Cudney-Valenzuela et al. 2023). As of 2020, approximately 10 million hectares of forest habitat were logged every year globally for timber extraction, agricultural expansion, and to mitigate tree loss from natural disasters, and this trend continues today (FAO 2020). Beyond direct habitat loss due to logging, changes in connectivity and edge characteristics increase accessibility for hunters and farmers. This leads to changes in species' behaviors, such as avoidance of certain areas (Tobler et al. 2018). To mitigate such spatial impacts and maintain the diversity and composition of forest animal communities, strategies focusing on habitat morphology, such as the preservation of unlogged patches and corridors, are necessary.

The morphology of logged areas (MLA) can be defined as the spatial structure of habitats where trees have been removed (i.e., areas in which the logged area represents the matrix) alongside with remnant areas from before the logging (i.e., unlogged area represents the patch) (Fig. 1). The fragment morphologies in logged forests (i.e., their compositions and configurations) can significantly influence wildlife distributions (Forman 1995; Linkie et al. 2008). The open environments created by logging expose vegetation to environmental factors, such as temperature,



Identifying morphologies of logged areas (MLAs) associated with medium and large mammal diversity and occurrence using landscape matrix analysis

Complex edges enhance accessibility from the matrix, increasing avoidance by forest species

Connected unlogged patches allow predators to move with less exposure and hunt more effectively

Fig. 1 Conceptual illustration of how different types of morphologies of logged areas (MLAs) may influence mammal diversity. **a** Logged areas with complex edges and fragmented unlogged patches may increase the exposure of predators to humans, leading to decreased diversity. **b** Logged areas with simpler shapes and well-connected unlogged patches may allow mammals to move with less exposure and hunt more effectively, increasing diversity light, and wind, increasing the growth of grasses while reducing the availability of shrubs and trees that serve as food, shelter, and cover for wildlife (Cudney-Valenzuela et al. 2023). As logging reduces the connectivity of tree-covered patches and creates more open areas, carnivores that rely on dense cover for hunting and shelter may struggle to survive (Iezzi et al. 2022). Increasing the edge complexity of forest patches elevates risks to forest-interior species by allowing greater human access to core habitats (Thornton et al. 2011). Conversely, ungulates may prefer logged areas where grasses thrive due to the lack of shade (Jamhuri et al. 2018).

While landscape metrics have been widely used to assess habitat fragmentation by classifying non-vegetated areas (e.g., developed land) as the matrix and vegetated areas as patches, few studies have specifically applied these metrics to assess the MLA (Fitz-Gibbon et al. 2007; Beltrão et al. 2024; Dennis et al. 2024; Pardo et al. 2024). In particular, studies defining logged areas as the matrix and unlogged remnants as patches to examine the effects of the MLA on medium and large mammal diversity remain limited. Landscape metrics, such as those implemented in the Fragstats software package, provide quantitative measures of habitat composition (e.g., patch-to-matrix proportions and counts) and configuration (e.g., edge complexity, spatial aggregation, and connectivity) (Liu et al. 2010; Do et al. 2022; Fragstats 2024). When applied to logged forests, these metrics can effectively capture MLAs by quantifying the proportion and spatial distribution of logged areas and evaluating the connectivity of unlogged patches. Specifically, the effective mesh size index can be used to assess whether well-connected patches better support mammal diversity than fragmented ones (Jaeger 2000; Girvetz et al. 2007).

The MLA may significantly affect the diversity of medium and large mammals, typically defined as species exceeding 1 kg in body mass (Sasaki and Ono 1994). Among landscape features, the edge density of logged areas and connectivity among unlogged patches are particularly influential. A higher proportion of unlogged forest within a species' home range may help it retain characteristics of the predisturbance habitat. In contrast, elevated edge density, resulting from intricately shaped logged areas, increases the length of the boundary between habitat types. Edges, especially those forming concave patch sections, can facilitate human intrusion, while protrusions of unlogged patches may increase environmental heterogeneity, potentially reducing the abundance of edge-sensitive mammal species (Slater et al. 2024; Fig. 1a). Conversely, high connectivity among unlogged patches can reduce exposure during movement and promote habitat use by facilitating access to essential resources under protective cover (Fig. 1b) (Pita et al. 2009; Lacasella et al. 2015; Acharya et al. 2017).

Different mammal species may prefer distinct unlogged patch morphologies, which would be reflected in their associations with various landscape indices (Oliveira et al. 2020). Key factors influencing these preferences include the area of unlogged patches within a species' home range, the degree of connectivity between unlogged patches, and the complexity of the shape of logged areas, i.e., whether they are simple and circular or complex. When unlogged patches are large and well-connected, conditions may be suitable for forest-interior species, allowing carnivores to move with reduced exposure to open areas (Michalski and Peres 2005). Conversely, when logged areas within the home range are highly complex in shape, edge species and herbivores may benefit by being able to graze on grasses in the open with nearby unlogged patches they can retreat to when predators approach (Forman 1995). Moreover, when logged areas are simple in shape, the distance from the center of an unlogged patch to its edge tends to be more uniform in all directions, resulting in a larger proportion of core area. This configuration allows forest-interior species to maintain their home range while minimizing encounters with habitat edges, reducing the frequency of exposure to human disturbance (Watson et al. 2004; Ruete et al. 2017).

This study aims to assess the impact of the MLA on medium and large mammals using nine landscape metrics that have not previously been applied to define MLAs. We test three hypotheses: (1) logged-area morphology metrics, particularly edge density and patch connectivity, represent effective indicators of habitat structure for medium and large mammals in logged forests; (2) these morphological metrics strongly correlate with mammal diversity in logged areas, with edge density negatively associated and patch connectivity positively associated; and (3) overall, the occurrence probability of most species tends to be higher in areas characterized by simpler edges and fewer open areas, which provide favorable conditions for habitat use.

Materials and methods

Study areas

We conducted mammal monitoring across six study areas covering 50 sites across seven mountains in South Korea (Fig. 2). These areas were selected because the varying logging intensities and morphologies within them create distinct differences in MLAs, which may differentially influence the diversity and distribution of medium and large mammals (Table 1). Among the six study areas, the mountains Gumi1 and Gumi2 include sites representing general, small-range logging practices, and the mountain Gumi3 and the Andong Mountains include sites representing salvage logging practices, in which burned trees were logged. The Chungju and Jeongseon mountains were mostly cleared, but some unlogged patches remain, as required by law when cutting areas over 5 ha.

All areas studied contained a variety of trees, including sawtooth oak (*Quercus acutissima*), cherry blossom (*Prunus sargentii*), Siberian silver birch (*Betula platyphylla*), Japanese larch (*Larix kaempferi*), and other species. In the unlogged patches, the most common deciduous tree species was oak (*Quercus variabilis*), and the most common coniferous species were red pine (*Pinus densiflora*), Korean pine (*Pinus koraiensis*), and Japanese larch (*L. kaempferi*) (Kim et al. 2017).

Nine medium or large mammal species are expected to inhabit the areas (Kang et al. 2016). These include three carnivores, leopard cat (*Prionailurus bengalensis*), Siberian weasel (*Mustela sibirica*), and yellow-throated marten (*Martes flavigula*); three omnivores, raccoon dog (*Nyctereutes procyonoides*), Asian badger (*Meles leucurus*), and wild boar (*Sus scrofa*); and three herbivores, water deer (*Hydropotes inermis*), roe deer (*Capreolus pygargus*), and the Korean hare (*Lepus coreanus*).

Monitoring wildlife using camera surveys

From April to October 2022, mammal distributions were monitored using camera traps at 24 logged sites and 26 unlogged patches across the study areas (Online Appendix S1). "Unlogged patch" refers to forested areas—excluding agricultural regions, such

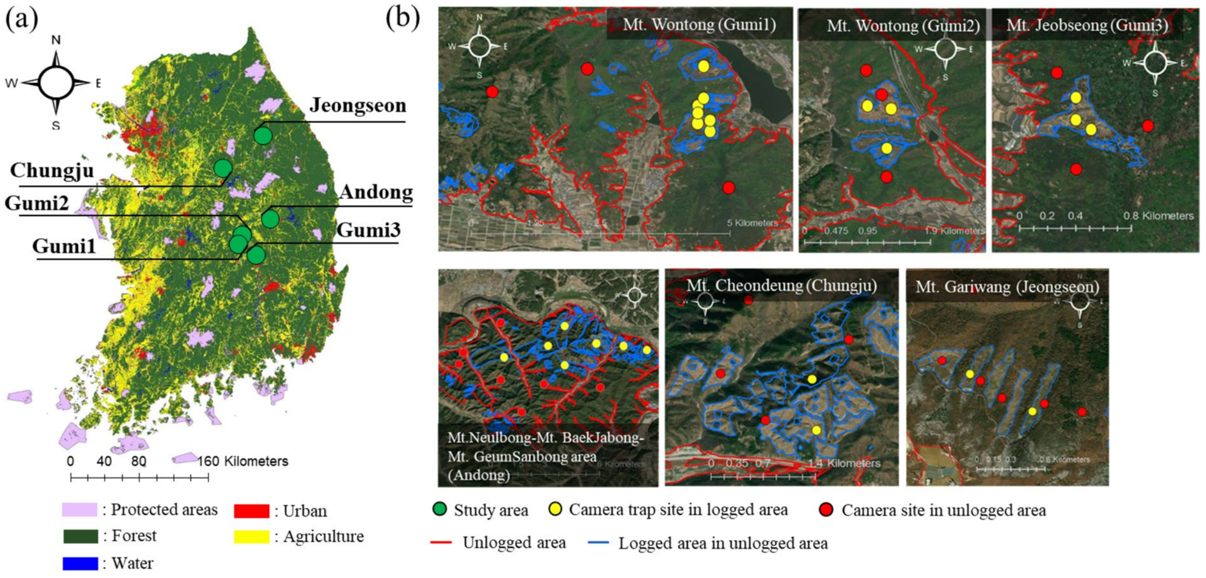


Fig. 2 **a** Six study areas (green circles) in South Korea. Land-use types are indicated by the color code below the map. **b** Satellite images of each study area showing logged areas (blue lines) and unlogged patches (red lines). Fifty camera trap sites were installed in the logged areas (yellow circles) and unlogged patches (red circles)

Table 1 Study area information. The elevation, slope, and aspect are the averages (± standard deviations) for the camera sites in each study area

Study area	[a]Year	[b]Area (ha)	Elevation (m)	Slope (°)	Aspect	Planted tree species
Gumi1	2018–2021	67	219 ± 74	12 ± 4	90 ± 37	Sawtooth oak (*Quercus acutissima*), cherry blossom (*Prunus sargentii*), Japanese larch (*Larix kaempferi*), and Siberian silver birch (*Betula platyphylla*)
Gumi2	2019–2022	33.02	229 ± 29	15 ± 2	91 ± 21	Cherry blossom (*Prunus sargentii*) and Siberian silver birch (*Betula platyphylla*)
Gumi3	2019–2022	27	208 ± 30	16 ± 4	234 ± 108	Cherry blossom (*Prunus sargentii*)
An-dong	2020–2022	1584	219 ± 48	11 ± 5	152 ± 97	Sawtooth oak (*Quercus acutissima*)
Chung-ju	2018–2020	205.3	391 ± 88	12 ± 5	196 ± 65	Sawtooth oak (*Quercus acutissima*), Korean red pine (*Pinus Densiflora*), and Japanese larch (*Larix kaempferi*)
Jeong-seon	2019	23	988 ± 36	19 ± 2	42 ± 36	Japanese larch (*Larix kaempferi*)

[a]the years in which logging occurred

[b]the total logged area

as orchards—where mature trees are left standing. "Logged area" typically denotes areas where trees have been harvested, excluding agricultural regions like roads, fields, and rice paddies. If new trees were planted after logging, the area was classified as logged if they contained young trees and low planting densities (i.e., if the area was relatively open). This ensured large differences in environmental characteristics between the logged area and the surrounding patches.

Camera trap sites were selected based on signs of a mammalian presence, such as footprints, scats, and rubbed trees. The mean minimum distance between sites within the areas was 651.47 m. Camera traps were affixed to tree trunks in unlogged patches or steel poles in treeless logged sites at heights of 0.7–1.2 m from the base (Lim et al. 2023). Cameras, including Browning BTC-6PXD (Browning, USA) and Stealth G42NG (Stealth, USA) cameras, were set up to take three consecutive pictures at 30 s intervals over the course of the upon being triggered and operated for at least one month at each study site. The locations of the cameras were recorded using a handheld global positioning system device (Garmin 64S, USA). Ultimately, we used data from 47 study sites that met the minimum monitoring period required to detect all mammal species (60 d), as determined by rarefaction analysis (Online Appendix S2; Si et al. 2014; Lim et al. 2023), for further analysis.

We calculated species diversity using the camera trap data, counting photographs of the same species within a 30-min period as a single occurrence to prevent the same mammalian individuals or groups of individuals from being counted repeatedly if photographed multiple times during a single appearance (O'Brien et al. 2003).

We applied a variation of the Shannon diversity index referred to as Hill number ^1D to identify influential factors that prevent the dominance of certain species and enhance overall diversity. If species dominance at a site is high, the index value is low, as ^1D quantifies diversity by considering species dominance in terms of equivalent numbers of equally abundant species (Alberdi and Gilbert 2019). Consequently, the modified index is considered more suitable for identifying environmental factors that mitigate species dominance and help maintain or increase overall mammal diversity. The Hill number ^1D diversity index was calculated using the equation.

$$^1D[0,9] = \exp\left[-\sum_{i=1}^{s}\left[p_i \times \ln\left(p_i\right)\right]\right]$$

where s indicates the number of species and p_i indicates the proportion of appearances represented by the i-th species.

Environmental variables of four categories

We collected data for 51 environmental factors potentially influencing species occurrence and categorized them into four groups (see Online Appendix S3 for details): (1) vegetation-related factors, indicating the availability of resources, including shelter, forage, and movement pathways; (2) anthropogenic factors, representing levels of human disturbance; (3) geographical factors, reflecting species-specific preferences for spatial or topographic features; and (4) MLA-related factors, capturing the potential of logged-area morphologies to mitigate exposure to predators or other risks.

We used 0.04 ha circles (radius: 11.28 m) centered on the camera trapping sites as the basic sampling unit to measure vegetation-related factors, including tree density, the volume of downed trees, and vegetation coverage, based on previous literature (Korea Forest Service 2019; Brown et al. 2020). Tree density was measured including trees with diameters at breast height (DBHs) over 6 cm. The volume of downed trees was calculated by multiplying their height by their basal area. Vegetation coverage was determined at six levels, ground cover (0–1 m), understory (1–2 m), midstory (2–8 m), overstory 1 (8–20 m), overstory 2 (20–30 m), and overstory 3 (> 30 m), in an imaginary vertical cylinder extending above the sampling site, and the coverage at each level was classified into one of four categories: 0, 0%; 1, 1–33%; 2, 34–66%, or 3, 67–100% (Lee et al. 2014). Anthropogenic variables included the distance from human-associated land-use types (urbanized area and road) and their areas within specific radii, calculated based on subdivided land cover maps with 1 m resolutions and 1:5,000 scales produced by the Ministry of Environment (2021). In this study, urban areas were defined as human-developed regions, including residential, industrial, and commercial land types, on the national land cover map (Ministry of Environment 2021). Among the geographical variables, aspect, slope, and altitude were extracted based on digital elevation models with 80 m resolutions and 1:5,000 scales produced by the National Geographic Information Institute of the Republic of Korea (NGII; Hong et al. 2020). Distances from inland water bodies and their areas within specific radii were determined using the same data sources as the anthropogenic variables.

The MLA was quantified using nine indices from the Fragstats software package (McGarigal and Marks 1995) characterizing the compositions and configurations of logged areas and unlogged patches. These indices were used to quantify the logged areas at each site, and a hypothesis associated with each index was defined (Online Appendix S3). To calculate the MLA indices, we classified the logged areas and unlogged patches (as, for example, seen in Fig. 1) within specific radii from each study site based on satellite images with approximately 1 m resolutions, along with field surveys.

As the effects of different factors on wildlife distributions may vary depending on the scale, we collected a subset of the anthropogenic (urbanized area and roads), geographical factors (water areas), and all MLA factors at the microscale (50 m radius), mesoscale (500 m radius), and macroscale (1 km radius) at each camera site (Farmer et al. 2006; Carvalho et al. 2018). For vegetation-related variables, there were practical difficulties with quantification at the three scales, so we only considered the basic unit (11.28 m radius; Korea Forest Service 2019; Brown et al. 2020). Since seven variables were not present within the radius of some study scales and, thus, had values of zero, despite their potential influence on mammals, we excluded them from further analysis. In analyses at all scales, variables with extremely broad ranges were log-transformed, and percentages were square root-transformed to improve normality and homogeneity of variance (Zar 1999).

To simplify the environmental variables, we conducted four separate principal component analyses (PCAs), one for each category, covering the 47 final variables (excluding ordinal variables). This approach allowed us to reduce the dimensionality of the data by extracting the principal components characterizing various aspects of the environment (see Online Appendix S4 for the correlation matrix of each category). We conducted the PCA across all three spatial scales simultaneously to identify the key environmental factors affecting mammal occurrence across these scales. Since PCAs group correlated variables into principal components, conducting the analysis across all three scales simultaneously helped identify which MLA factors are highly associated with each other and which are independent (do Carmo Ponzio et al. 2024; Victorel et al. 2024). For example, if the MLA within 500 m and 1 km had no correlation, they would be grouped into separate principal components. We selected significant principal components as those with eigenvalues exceeding one, following the Kaiser criterion (Mangas and Rodríguez-Estival 2010). We identified the most strongly associated variables for each component after performing a varimax rotation. Specifically, we focused on variables with loadings higher than 0.6 in the significant with eigenvalues above 1 rotated principal components to interpret the analysis results (Santiago et al. 2022). The PCA and varimax rotation were conducted using the *psych* package in R (Ramesh et al. 2016).

Correlated components were identified and removed using the “vif” function from the *usdm* package, which calculates the variance inflation factor (VIF) for all variables. This function iteratively excludes the component with the highest VIF until no variables exceed a specified threshold (in this case, “vif = 3”) (Naimi et al. 2014; Online Appendix S5). Once this process was completed, 16 variables were retained (11 PCA components and five ordinal factors).

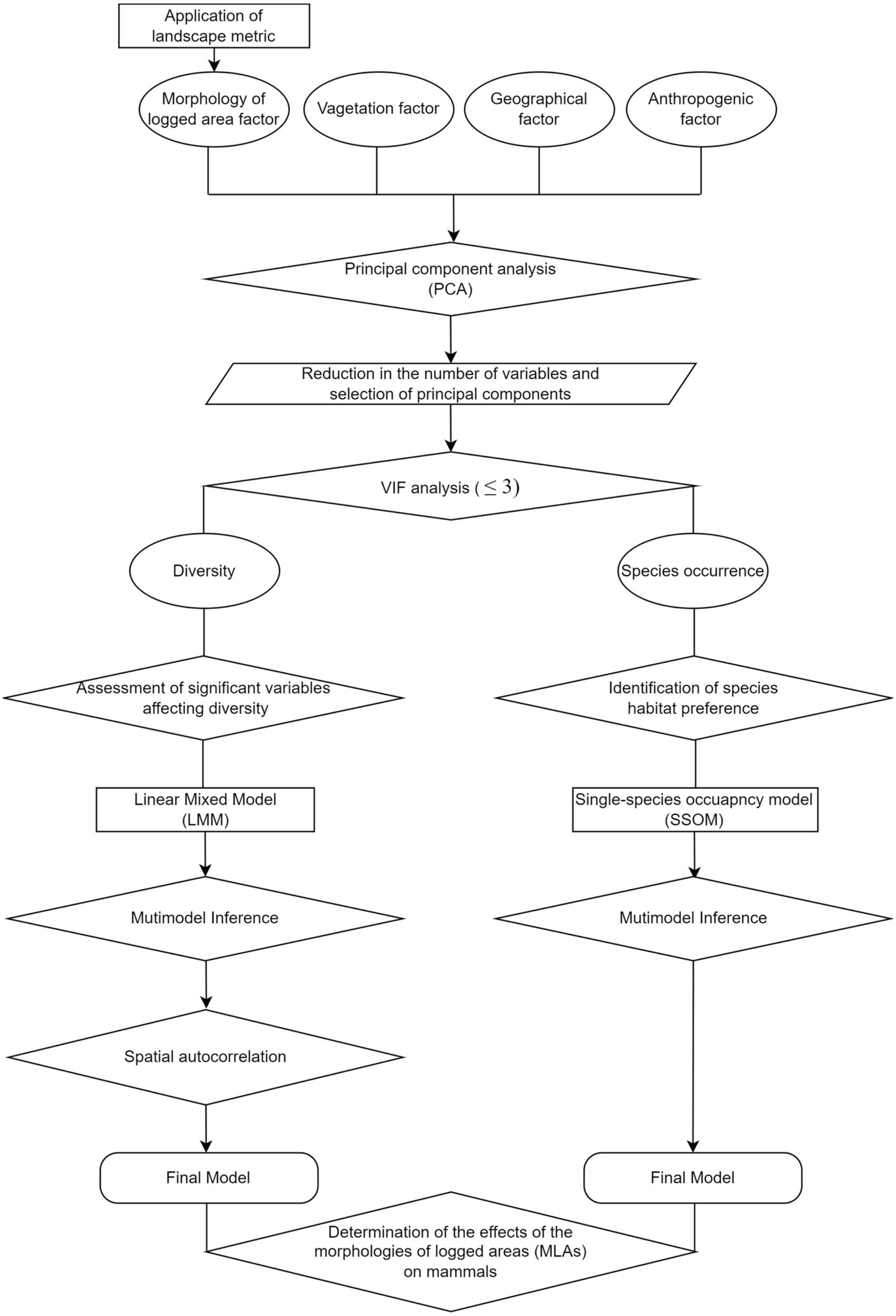
Lastly, detection-related covariates that might affect detection probability were collected: (1) the camera model; (2) the operator, i.e., the person who installed the camera; and (3) the number of monitoring days. While both camera models had similar capabilities, potential differences in detection probability due to variations in specifications (e.g., sensor sensitivity or trigger speed) were considered. Additionally, while we followed a standardized protocol to ensure consistency in camera placement (e.g., fixed height) to minimize operator effects, minor variations in installation by different operators may have occurred.

Data analysis

We used linear mixed models (LMMs) to identify the environmental factors influencing mammalian diversity (Fig. 3). These models are particularly suitable for analyzing relationships between continuous response variables (e.g., mammalian diversity) and environmental predictors while accounting for random effects. In our study, camera model and operator were treated as random intercepts to account for any possible variability in detection caused by these factors (Hong et al. 2020). The LMMs enabled us to examine the fixed effects of 16 environmental variables while considering site-level variability, providing robust estimates of relationships relevant to mammal diversity. While observation days could also affect detection probability, this factor was already accounted for in the calculation of diversity values.

We applied a variable selection procedure to compare models with all possible combinations of the 16 covariates using the “dredge” function of the *MuMln* package (Barton 2018; Online Appendix S6). Due to our computer capabilities, we could not proceed with all combinations of the 16 environmental variables at once. Therefore, we divided the variables into two groups of eight and ran the “dredge” function on each group separately. Then, in each operation, we averaged the models for which the ΔAICc values were less than 2 based on a small-sample corrected Akaike’s information criterion (AICc) (Anderson and Burnham 2004; Hong and Joo 2021). To select the explanatory variables, we retained only those that were statistically significant ($p < 0.05$) from each averaged model (MacNally 2000). After this initial screening, we combined the significant variables from both groups and re-ran the model selection process on the reduced set of variables, as the total number of covariates was then manageable. Through this variable selection procedure, we identified the most parsimonious model or, applying model averaging to derive the final estimates if multiple models showed similar support (ΔAICc < 2; Hong and Joo 2021). The percentage of deviance explained (%DE) was used to indicate the explanatory power of the final model. To assess spatial autocorrelation in the model residuals, we extracted residuals and tested for spatial dependence using Moran’s I. A spatial weights matrix was constructed based on a GAL file generated using the GeoDa software (1.22.0.4), and the significance of Moran’s I was evaluated via a Monte Carlo permutation test ($n = 999$) using the *ncf* and *spdep* packages in R (García et al. 2014).

To identify the naïve habitat preferences of each species, we used a single-species occupancy model (SSOM) to examine the relationship between occupancy probability and the environmental variables (Fig. 3). These models were used to estimate species-specific occupancy probability (ψ) and detection probability (p) for each species independently. This approach is advantageous because it accounts for imperfect detection, a common issue in wildlife surveys. By modeling species’ occurrence probabilities separately, SSOMs allow for a more nuanced understanding of how environmental variables, including MLA characteristics, influence each species’ habitat preferences, even when detection is not guaranteed (Fiske and Chandler 2011; MacKenzie et al. 2022).


Application of landscape metric
Morphology of logged area factor
Vagetation factor
Geographical factor
Anthropogenic factor
Principal component analysis (PCA)
Reduction in the number of variables and selection of principal components
VIF analysis (≤ 3)
Diversity
Species occurrence
Assessment of significant variables affecting diversity
Identification of species habitat preference
Linear Mixed Model (LMM)
Single-species occuapncy model (SSOM)
Mutimodel Inference
Mutimodel Inference
Spatial autocorrelation
Final Model
Final Model
Determination of the effects of the morphologies of logged areas (MLAs) on mammals

◂**Fig. 3** Diagram of the data analysis procedure for identifying the relationships between environmental factors, including the morphology of logged area indices, and mammal diversity and species occurrence frequency using linear mixed models and single-species occupancy models, respectively

In this process, the detection history of each mammal species at each site—i.e., the sequence of the species detection/non-detection data at each date in the camera capture data, binned into 10-day detection or non-detection bins—was used as a response variable in the model. Sixteen environmental variables affecting occupancy probability (11 PCA components and five ordinal factors) and three environmental variables affecting detection probability (camera model, operator, and the number of monitoring days per bin) were considered. We performed the same model selection process as was used for the LMM analysis to identify the most parsimonious (single or averaged) single-species occupancy models (Barton 2018; Anderson and Burnham 2004, Online Appendix S7).

Results

Environmental variable reduction using principal component analysis

Twelve significant components were extracted from separate PCAs conducted for each of the four previously defined categories (Online Appendix S8): one vegetation-related component (FO), three anthropogenic components (AN1–AN3), two geographical components (GE1 and GE2), and six components representing logged-area morphology (ML1–ML6). The component FO reflected greater logging intensity. The anthropogenic components captured different aspects of human disturbance: AN1 represented urbanized areas, AN2 captured areas located farther from roads, and AN3 reflected areas farther from trails. The geographical components were associated with proximity to water bodies, with GE1 indicating greater distances from water and GE2 characterizing water-dominated areas at the macroscale.

The MLA factors showed distinct associations with spatial scales and with specific variable groupings (Online Appendix S8). Variables representing the 50 m scale were clearly separated into ML1, whereas variables at the 500 m and 1 km scales were grouped together within ML5. Regardless of spatial scale, specific MLA characteristics were strongly associated with each component. In both ML1 and ML5, the ratio of logged area, maximum edge length ratio, and effective mesh size were highly influential variables. The shape index of logged areas appeared in both ML4 and ML6; in ML4, the minimum distance between adjacent logged areas was important, whereas ML6 was linked to the number of logged areas.

Factors influencing the diversity of mammal species occurrences

A total of nine species, all expected to inhabit the survey sites, were observed, with a mean occurrence frequency of 0.8 ± 0.1 (the occurrence per total of 162 camera days) across the six areas (Online Appendix S9). Among the 325 LMMs tested, the most parsimonious model showed that the diversity index (^{1}D) increased as the proportion of logged areas and edge complexity decreased within the microscale radius (ML1: -0.43 ± 0.12 [coefficient ± standard error], $p < 0.001$; Fig. 4; Online Appendix S6). This model accounted for 23% of the deviance in diversity within the LMM analysis, and the residuals of the model did not demonstrate significant spatial autocorrelation ($p > 0.05$).

Species-specific relationships between occupancy probability and environmental variables

Based on the most parsimonious SSOMs, some meso-predators and omnivores were influenced by ML components and the FO component (Fig. 5), while herbivore occurrences were not associated with any environmental variables. The AN and GE components did not significantly influence species-level occupancy.

For wild boar (*S. scrofa*), the most parsimonious model among 1,048 candidate combinations indicated that a lower proportion of logged areas and simple edges at the microscale (ML1)—also identified as a significant predictor of diversity in the LMM—negatively affected occurrence ($\beta = -1.76 \pm 0.65$, $p < 0.01$; Online Appendix S7). For Asian badger (*M. leucurus*),

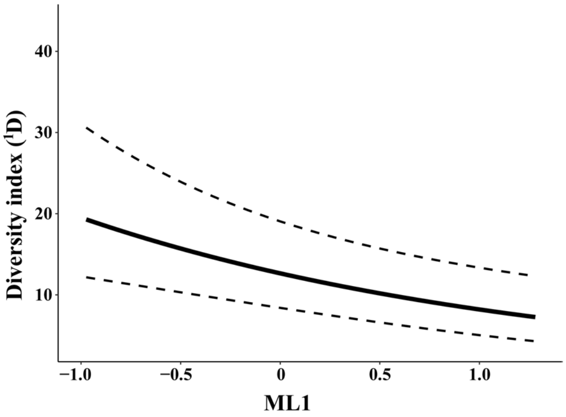


Fig. 4 Relationship between the mammal diversity index ^{1}D and the most influential environmental variable from the most parsimonious model selected via multi-model inference. The solid line represents predicted values of the diversity index, and the dashed lines indicate the 95% confidence interval. The x-axis represents ML1, a principal component derived from a principal component analysis of logged-area morphology variables. It is negatively associated with landscapes characterized by extensive logged areas with complex edges within a 50 m radius

the most parsimonious model among 1,028 combinations showed a similar negative association with ML1 ($\beta = -0.80 \pm 0.36$, $p < 0.05$). For leopard cat (*P. bengalensis*), the most parsimonious model among 1,026 combinations revealed a negative relationship with ML6, which represents complex logged-area morphologies at the macroscale ($\beta = -1.22 \pm 0.45$, $p < 0.01$). For raccoon dog (*N. procyonoides*), model averaging across the top two models (ΔAICc<2) indicated a strong negative association with FO, which represents greater logging intensity ($\beta = -1.32 \pm 0.16$, $p < 0.001$).

Five species—water deer (*H. inermis*), roe deer (*C. pygargus*), Korean hare (*L. coreanus*), yellow-throated marten (*M. flavigula*), and Siberian weasel (*M. sibirica*)—were not significantly influenced by any environmental variables in their best-supported models. Water deer and roe deer were frequently observed across most sites (water deer: 370 detections [66%] across 42 sites [89%]; roe deer: 278 detections [49%] across 42 sites [89%]), whereas the other three species appeared infrequently (yellow-throated marten: 20 detections [4%] across 13 sites [28%]; Korean hare: 12 detections [2%] across 5 sites [11%]; Siberian weasel: 12 detections [2%] across 4 sites [9%]).

Discussion

To the best of our knowledge, this study is the first to identify the morphology of logged areas (MLA)—defined by nine landscape metrics describing the spatial configuration of logged areas and unlogged patches—as the most influential factor affecting the diversity of medium and large mammals. MLA-related variables surpassed other environmental categories, including forest, anthropogenic, and geographical factors. When environmental variables were reduced to 12 principal components, the most influential components affecting both species diversity (ML1) and species-specific occurrence (ML1, ML6, and FO) consistently corresponded to MLA-related components. These results suggest that mammal habitat use is particularly sensitive to the morphological characteristics of logged areas, such as unlogged patch connectivity, edge complexity, and patch distribution, especially when anthropogenic disturbances are present nearby. Previous studies have shown that even logged forests near urban areas can still support wildlife if they offer movement corridors and food resources through unlogged patch connectivity (Brodie et al. 2015; Bovo et al. 2018). Similarly, if the patch structure around water sources increases exposure to predators or facilitates human access, water-dependent species tend to avoid those areas (De Boer et al. 2010; Slater et al. 2024). Our findings indicate that in landscapes where multiple habitat factors interact, MLA characteristics can play a disproportionately important role in shaping mammal distributions.

When the four environmental variable categories were analyzed separately using PCAs, MLA factors exhibited distinct associations based on spatial scale. Specifically, variables at the 50 m scale were linked with one component, ML1, while those at the 500 m and 1 km scales were linked with another, ML5. This likely reflects stronger variation in logged area configurations at fine scales, with distinct sets of interrelated variables at each scale. Microscales, such as the 50 m scale, representing highly localized habitat structure, differ from broader spatial scales that tend to reflect more homogeneous landscape characteristics (Wu and Qi 2000). Though at different scales, components ML1 and ML5 shared several key MLA indices—namely, the ratio of logged area, the maximum edge length ratio, and the effective mesh

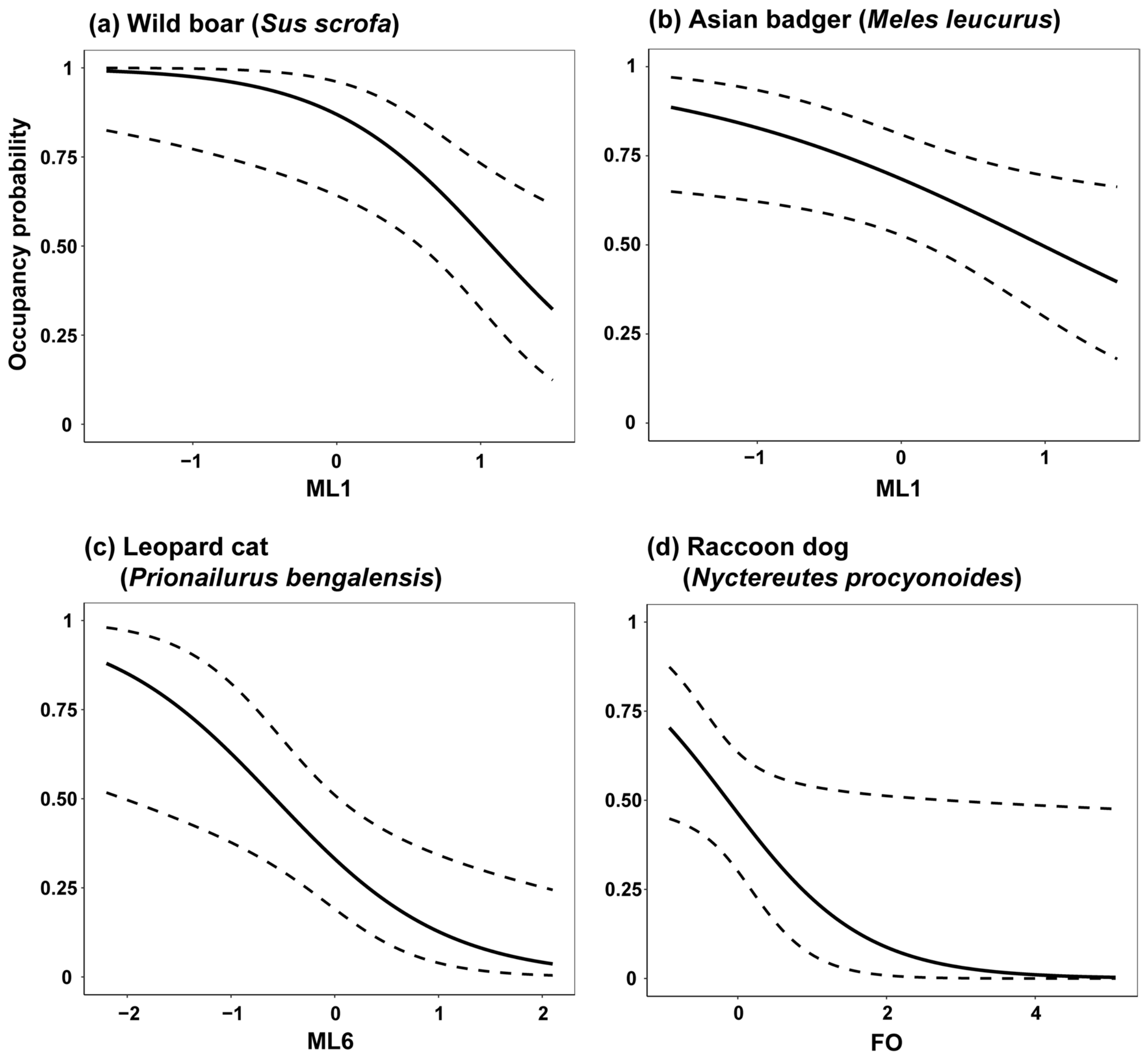


Fig. 5 Standardized coefficients showing the relationships between significant environmental variables and occupancy probabilities for four species, based on single-species occupancy models: wild boar (*Sus scrofa*; **a**), Asian badger (*Meles leucurus*; **b**), leopard cat (*Prionailurus bengalensis*; **c**), and raccoon dog (*Nyctereutes procyonoides*; **d**). Solid lines indicate predicted values, and dashed lines represent 95% confidence intervals. The variables ML1 and ML6 are principal components derived from a principal component analysis (PCA) of logged-area morphology (MLA) variables, representing a lower proportion of logged areas and simpler edges at the 50 m scale and logged area complexity at the 1 km scale, respectively. The variable FO is a principal component derived from vegetation-related variables representing logged areas characterized by lower tree densities and more downed trees

size—all of which were consistently associated across spatial scales. These metrics, which characterize edge density and patch connectivity relative to total forest area, are inherently sensitive to spatial scale (Šímová and Gdulová 2012). In practice, South Korea's Sustainable Forest Management Guidelines require the retention of circular (minimum 25 m radius) or strip-shaped (minimum 20 m width) unlogged patches within logged forests, which may contribute to increased heterogeneity at the 50 m radius (Korea Forest Service 2024). Additionally, lower connectivity tends to result from a higher proportion of logged areas, possibly explaining why these indices tended to be grouped together across scales (Justeau-Allaire 2024). Components ML4 and ML6 were closely associated with the logged area shape index, representing the complexity of logged area distribution. This index was associated with either the minimum distance between adjacent logged areas or the number of logged areas, respectively. In heterogeneous environments with high logging complexity, a greater number of logged areas with complex edges are more likely to be present, and distances between logged areas are likely to be greater (Perović et al. 2015).

Using landscape metrics that quantify the MLA, we found that diversity could increase in habitats with simple edges and high connectivity (Fig. 4). Supporting this, variables significantly contributing to ML1 (the edge characteristics of logged areas within the microscale radius) were strongly negatively associated with diversity, showing that biodiversity increased with shorter total edge lengths, smaller edge proportion in the largest logged area, fewer logged areas, and higher connectivity within 50 m. Mammals tend to thrive in areas where the logged areas are relatively circular and simple, which creates a relatively uniform distance from the unlogged patch's core to its edge (Watson et al. 2004; Ruete et al. 2017). Regions with these logging patterns tend to feature well-connected mature forest environments, creating closed areas for herbivores to rear offspring and migrate to larger and more stable unlogged patches, ultimately improving survival rates (Schippers et al. 2014; Marchand et al. 2015). Additionally, such environments offer carnivorous predators an ideal environment to hunt prey under tree canopies or within dense vegetation, providing refuge from human disturbance (Murray et al. 1995). Consequently, these characteristics attract wildlife, leading to increased biodiversity.

According to the SSOM results, three mesopredator and omnivore species showed significantly lower occupancy probabilities in environments with a higher proportion of logged areas and more complex edges (Fig. 5). Two MLA-related PCA components were influential, with ML1 negatively affecting the occupancy of the omnivorous wild boar (*S. scrofa*) and Asian badger (*M. leucurus*) and ML6 negatively affecting the occupancy of the carnivorous leopard cat (*P. bengalensis*). Derived from microscale data (50 m), greater ML1 values reflect landscapes with larger unlogged patches interspersed with logged areas having simple, compact edges—conditions that promote local connectivity. Such structures likely offer both stable shelter and food resources, including tree fruits and invertebrates, which are beneficial to omnivores like wild boar (*S. scrofa*) and Asian badger (*M. leucurus*) (Ballari and Barrios-Garcia 2014; Bae et al. 2021). While wild boars (*S. scrofa*) are often observed near agricultural lands, they may prefer well-connected unlogged patches in logged landscapes due to higher resource availability and reduced risk of exposure (ENETWILD consortium et al. 2019; Zhang et al. 2024). In contrast, leopard cats (*P. bengalensis*), which primarily hunt small mammals, were most influenced by ML6—a component associated with logged area complexity at the macro scale (500 m and 1 km). They showed a preference for areas with fewer logged areas, lower total edge lengths, and simpler spatial distributions, which may facilitate long-distance movement and enhance ambush success by minimizing exposure to open areas (Ghimirey et al. 2023; van der Meer et al. 2023). Raccoon dogs (*N. procyonoides*) showed lower occupancies in logged forests with high volumes of downed trees, likely due to their preference for denser cover that provides better foraging and shelter opportunities (Wooldridge et al. 2024).

Only omnivores and carnivores exhibited clear, significant habitat preferences, suggesting they are more sensitive than herbivores to disturbance. Three out of four of these species were influenced by the MLA, whereas no significant variables related to habitat preference were identified for the three herbivores (water deer [*H. inermis*], roe deer [*C. pygargus*], and Korean hare [*L. coreanus*]). Omnivores, relying on both plants and prey as food resources, may be more sensitive to logging since it affects their primary resource availability, requiring them to adjust their foraging strategies as the habitat changes (Hämäläinen et al. 2022; Eubanks and Denno 1999). In addition to these factors, carnivores also tend to avoid open environments to enhance ambush hunting success (Murray et al. 1995; Mills and Mills 2014; Jo and Baccus 2016). In highly heterogeneous landscapes with stark contrasts, such as those seen between logged areas and unlogged patches in terms of vegetation height and openness, these species may behave differently than they do in more connected environments, restricting movement and reducing home ranges (Poessel et al. 2014). In contrast, the herbivores (excluding the Korean hare, which had low detection rates), such as water deer (*H. inermis*) and roe deer (*C. pygargus*), showed no clear habitat preference but were detected at 89% of the sites. This suggests that herbivores may be less sensitive to anthropogenic disturbance in forests (Berger 2007; Tinoco et al. 2011).

Morphological characteristics related to connectivity and edge density within a 50 m radius (ML1) had a significant impact on mammal diversity and the occupancy of multiple species, whereas those associated with patch count and shape complexity at broader spatial scales (ML6) affected only one species. This suggests that mammals may respond more strongly to environmental heterogeneity at finer scales, particularly when navigating toward safe buffer zones to avoid predation or human disturbance (Kie et al. 2002; Monroe et al. 2022). In fragmented forest landscapes, wildlife often moves in search of secure habitats that mitigate food scarcity and exposure to threats. However, at the species level, some predators—such as the leopard cat (*P. bengalensis*)—may rely more heavily on broader-scale environmental features to maintain viable home ranges (Huffaker et al. 1963; Sih and Christensen 2001). These findings highlight the importance of considering MLA factors across multiple spatial scales when examining wildlife distributions, as species-specific ecological traits shape their responses to habitat structure.

Limitations and further research directions

Long-term monitoring is essential, not only for dynamically monitoring changes in MLA patterns but also for observing how these changes affect species interactions and population dynamics. Over time, vegetation coverage in logged areas may become similar to that in unlogged patches, with shrubs becoming taller and trees planted through afforestation ultimately reforming the high canopy (Huth and Ditzer 2001; Ng et al. 2021). As this occurs, adjustments to the composition and configuration of previously logged areas could be made, with some eventually being reclassified as unlogged patches, and variables, including MLA indices, could be recalculated (Schulz et al. 2010). Such changes in MLA patterns could alter their effects on mammals, particularly as the boundaries between logged areas and unlogged patches shift due to vegetation growth. This long-term monitoring would also help assess whether the same indices continue to affect mammal populations and communities over time. Additionally, it could provide insights into the habitat preferences of species with insufficient sample sizes for occupancy analysis due to low detection rates, such as the Siberian weasel (*M. sibirica*), yellow-throated marten (*M. flavigula*), and Korean hare (*L. coreanus*).

Vegetation coverage, based on a 0.04 ha area centered on each camera, was identified as an important factor for certain species. However, the area covered by the vegetation surveys may be too small to fully capture the home ranges of medium and large mammals (Zhou et al. 2008). High tree densities provide a dense canopy that may serve as ambush sites for some predators while offering refuge corridors for prey species (Murray et al. 1995; Lee et al. 2014). In contrast, areas with abundant downed trees tend to have lower tree densities, fewer food and shelter resources for forest-dwelling species, and open environments that some predators may avoid, possibly explaining why raccoon dogs (*N. procyonoides*) in our study showed lower occupancies in such areas. On the other hand, because mammals perceive and move based on their immediate surroundings rather than their entire home range, the presence of individuals at camera points may indicate that the nearby vegetation provides a suitable environment within their home range (Gehring and Swihart 2003; Korea Forest Service 2019). Yet, since the vegetation survey range in this study is relatively small compared to the home ranges of the studied mammals (e.g., 4.01 km^2 for wild boar [*S. scrofa*], Fattebert et al. 2017; larger than 3.69 km^2 for leopard cat [*P. bengalensis*], Choi and Park 2009; and 2.78 km^2 for water deer [*H.inermis*], Kim and Lee 2011; etc.), future research should consider these limitations when conducting more in-depth studies.

Management implications

Among the habitat factors, we found that MLA factors significantly impact wildlife diversity. This suggests that logging practices should focus not only on preserving residual forest areas but also on designing the shapes and determining the appropriate extents of logged areas. According to the UN Sustainable Development Goals (UN-SDGs), maintaining and protecting terrestrial biodiversity is a key global management objective (United Nations 2023). Since banning the use of forest resources through logging is not feasible, there is a need for spatial management strategies that balance sustainable resource use and biodiversity conservation. Therefore, to maintain biodiversity, logging operations should ensure well-connected logged areas with simple edges at a microscale (50 m) and consider a simplified morphology at larger scales, particularly in sensitive predator species' habitats.

Conclusions

In six forested regions in Korea containing logged areas, we investigated the relationships between medium and large mammal diversity and occupancy and landscape indices characterizing the morphology of logged areas (MLA). Among the four environmental factor categories, MLA indices had the most substantial effects on mammals. To the best of our knowledge, this study is the first to define and quantify the MLA as a distinct framework for assessing mammal responses to logging. Enhancing habitat connectivity through simplified edges and well-connected unlogged patches at the microscale—along with strategic planning of the MLA at broader scales—may help mitigate the ecological impacts of logging. Incorporating MLA indices into forest management strategies could play a key role in supporting mammal conservation in logged forests.

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Declarations

Competing interests The authors declare no competing interests.

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